EFFECTS OF DIFFERING RESPONSE-FORCE REQUIREMENTS ON FOOD-MAINTAINED RESPONDING IN CD-1 MICE

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The effect of force requirements on response effort was examined using outbred (CD-1) mice trained to press a disk with their snout. Lateral peak forces greater than 2 g were defined as *threshold* responses (i.e., all measured responses). Different force requirements were used to define *criterion* responses (a subclass of threshold responses) that exceeded the requirement. The reinforcer was sweetened, condensed milk, and it was delivered upon response termination. All mice were exposed to two ascending series of criterion force requirements (2, 4, 8, 16, and 32 g). Increasing the force requirement decreased criterion response rates, but increased threshold response rates. The time-integral of force (area under the force–time curve for individual responses, which is proportional to energy expenditure for each response) increased with the increase in the force requirement. These results conflict with the hypothesis that higher force requirements have aversive qualities and suggest that increased force requirements are more analogous to intermittent schedules of reinforcement. These data suggest that estimations of effort or energy expenditure should be measured independently of the force requirement. Individual differences in responding were found for the CD-1 outbred stock.

Key words: operant, effort, force, disk press, CD-1 mice

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The aims of the present experiment were to address the proposition that increases in response effort are aversive, that is, that they decrease operant responding much as punishing stimuli do (Alling & Polling, 1995) and to identify the technical and methodological requirements needed to address this question. All behavior requires time and effort, but while the temporal dimensions of behavior have been measured extensively, the analysis of effort has received little attention (Alling & Poling; Fowler, 1987). In part, the lack of attention to response effort may be due to the difficulty of accurately measuring this behavioral dimension.

Measurement of the temporal dimensions of responding is basically complete once the operational definitions of when a response begins and ends have been specified. However, additional factors must be addressed in the measurement of effort. To understand these factors one must first define effort in terms of the physical properties of force, work, and heat. Force is the effect on the state of rest or motion of matter. Work only occurs when matter is displaced a finite distance by the application of a force (work = force × distance). However, not all forces result in work. In the case of a key or lever press, force can still be applied to the operandum even though the key or lever is fully depressed. At this point the force applied to the operandum does not result in work, but results in metabolic heat in the muscles that is dissipated into the environment (see Notterman & Mintz, 1965; Trotter, 1956, for details). The forces that result in both work and heat must be accounted for if an accurate estimate of effort is to be achieved.

Most studies on effort have required a subject to move different weights a fixed distance (i.e., work). Experimenters inferred that moving a heavy weight a given distance a certain number of times required more effort than moving a lighter weight the same distance and number of times. To automate the measurement of effort, a response lever was attached to a microswitch. When the lever was moved a specified distance, the microswitch was activated and a response was recorded. Weights then were added or removed from

the opposite side of the lever to manipulate the force requirement. This method manipulated effort as an independent variable (i.e., force requirement), inferred from the movement of different weights the same distance. The dependent variable in this method was response rate on the levers with different weights.

There are three possible events that produce inaccuracies using this method of estimating effort. First, lever presses that move a weight, but not enough to activate a microswitch (i.e., subcriterion responses) were not counted even though physical work was accomplished. Second, pressing a lever harder than necessary (i.e., supracriterion force when a lever reaches its limit of travel) to activate a microswitch does not produce work, but does result in metabolic heat produced by the muscles involved in the response. And third, continuing to hold a lever once maximum travel has been achieved also results in metabolic heat. In these situations, energy is expended (i.e., effort) but not measured, resulting in an underestimation of response effort.

To deal with these limitations, Notterman and Mintz (1965) pioneered the measurement of response force as a dependent variable separate (i.e., not inferred) from the force requirement used as the independent variable. This method used strain-gage and computer technology to measure directly the force applied to an operandum. In this set up, all forces above a threshold (minimum detectable force) were recorded (i.e., threshold responses) and reinforcement contingencies could be programmed for different dimensions of a response (e.g., peak force, response duration, time integral of force). Thus, all responses above a detection threshold were measured, allowing a better estimate of effort. In addition, Notterman and Mintz advocated the use of the ''time-integral of force'' as a more complete estimation of response effort. The time-integral of force sums the force emitted across time from the beginning to the end of a defined response, providing an estimate of total effort output. In physiological preparations, the time-integral of isometric force has been shown to be proportional to energy utilization by striate muscle (Jobsis & Duffield, 1967). Another important feature of this measurement system is that responses that do not meet the reinforcement criterion are also recorded (i.e., threshold responses) allowing for measurement of the broader operant class that is engendered by the reinforcement contingencies used to generate responses (Catania, 1998).

Estimating effort is important because of its relation to the psychological construct of ''value.'' At a simple level, one can infer the value of a commodity to an organism from how much effort is expended in acquiring that commodity. The amount of behavior that produces the commodity defines the price or cost of the commodity. This inference is the basis for using progressive ratio schedules (e.g., Richardson & Roberts, 1996; Stafford, LeSage, & Glowa, 1998) in which the price (number of lever presses) increases after each reinforcer. In addition, most learning theories either implicitly or explicitly recognize a principle of least effort (Killeen, 1995), which suggests that learning involves a refinement of performance so that an efficient form of responding develops. The principle of least effort implies that reinforcement contingencies requiring high amounts of effort (e.g., large fixed ratios or force requirements) may have aversive qualities that would have punishment-like effects on effortful operant behavior (Blough, 1966; Chung, 1965; Miller, 1968; Solomon, 1948). Alling and Poling (1995) systematically investigated the extent to which increasing a force requirement on lever presses decreased lever press rate and suggested that increasing the physical effort required to emit a response increased the aversiveness of responding, thereby decreasing responding, comparable in some regards to punishment. The authors noted, however, that their apparatus could not measure lever presses that did not meet the force requirement and suggested that future experiments might utilize equipment capable of measuring the actual force of each response and to show how force distributions change as a function of the force requirement.

The development of a computer automated force measurement system (Zarcone & Fowler, 2001) based on the behavioral measurement concepts introduced by Notterman and Mintz (1965) now makes it convenient to analyze force as both an independent (force requirement) and dependent (peak force, time integral of force) variable in the same preparation. The main purpose of the present

experiment was to use isometric load-cell technology to measure all responses above a predefined measurement threshold (threshold disk presses) as well as responses that met the force requirement (criterion disk presses) thereby quantitating effort expended under increasing force requirements during a fixed-ratio 1 schedule of reinforcement.

Another purpose of this experiment was to examine the behavior of mice in a group design that typically is used when comparing different strains or stocks of mice. Before comparing different inbred strains of mice, our strategy was to examine, in detail, the behavior of the outbred CD-1 stock, which is similar to outbred rat strains typically used in rodent behavioral studies. The CD-1 outbred stock has received less behavioral attention than inbred mouse strains (e.g., BALB/cJ, C57BL/6J, 129x1/SvJ), due to greater genotypic variability and potential behavioral phenotypic variability (Festing, 1999; McClearn, 1999; Miller et al., 1999), which can complicate between-group experiments looking for specific gene–behavior relations. Even though the CD-1 stock cannot represent all the potential alleles for mice, the allelic diversity of this stock is greater than that of inbred strains, and this diversity can be useful in providing the covariance needed for the examination of genetic and environmental influences on behavioral phenotype (McClearn). Some of the studies that have examined the behavior of the CD-1 stock have reported them to be, on average, good at the T-maze continuous alternation task, good in discriminated avoidance learning using a Y-maze task or the Morris water maze, and they froze less (than the C57BL/6 inbred strain) during cue-dependent fear conditioning (Gerlai, 1998; Gerlai, Adams, Fitch, Chaney, & Baez, 2002).

METHOD

Subjects

Outbred CD-1 (n=12, Charles River Laboratories) male mice were purchased at 7 weeks of age and group housed in quarantine at the animal-care facilities for 7 days prior to being housed individually in home cages for 15 days with ad-lib food and water. Then, access to dry food was restricted to 3 hr daily, starting at approximately 5 pm, with water still freely available. Training began 13 days later (mice approximately 13 weeks old). All procedures were carried out in accordance with the *NIH Guide for the Care and Use of Laboratory Animals* and were approved by the University of Kansas Animal Care and Use Committee.

Apparatus

Eight customized operant chambers were each enclosed in separate painted double-walled plywood sound-attenuating boxes with exhaust fans (Zarcone & Fowler, 2001). An intelligence panel mounted on one wall of each chamber (23.5 cm long × 21.5 cm wide × 18.5 cm high) held the response and stimulus devices. A force-sensitive aluminum disk (attached to the sensing shaft of a Model 31 Sensotec load cell with a 0-250 g range) was recessed 0.1 cm behind a 0.5 cm diameter hole, located below the houselight, 1 cm above the cage floor (see Figure 1). The orientation of the force disk close to the floor and behind the intelligence panel was an attempt to limit access to the disk by only the snout. Repeated observations throughout the experiment through the chamber peephole confirmed that only the snout was being used to depress the disk. Force–time waveform data, produced by presses to the disk, were measured via a computer-controlled, analog-to-digital converter that recorded at a sampling rate of 100 samples per s with a 0.2 g resolution. Disk-press force was defined in gram equivalent weights (1 g = 0.098006 N), because gram weights were used to calibrate the force sensors. Separate measures of disk-press responding (e.g., peak force, duration, and rate of disk presses), were computed online, and could be used to establish the criterion for reinforcement.

An electromechanical dipper (Gerbrands, G5600 GS-RH) mounted outside the cage presented 0.05 ml of sweetened condensed milk (one part milk/two parts water), which served as the reinforcer, for 5 s via a hole located in a reinforcer hopper. Activation of the dipper produced a loud clap when the stop on the solenoid shaft abruptly hit the steel collar on the solenoid coil. Dipper activation also produced a vibration detectable by human finger tips pressed against the grid floor. The force transducer operandum was mechanically isolated from this vibration. In our procedure, the stimuli signaling reinforcement delivery
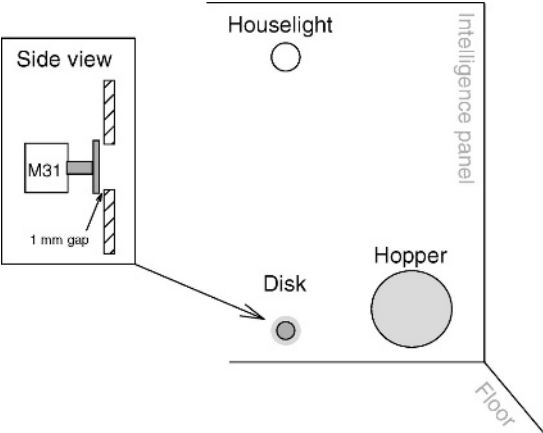
Fig. 1. Drawing of the intelligence panel used in the operant chambers. The bottom of the force disk hole was located 1 cm above the chamber floor. Both the houselight and force disk hole were centered on the intelligence panel 9.25 cm from either side wall.

(auditory clap and vibration) occurred within 10 to 30 ms of a criterion response. The hopper, 5.5 cm diameter, 3 cm deep, was mounted 3.5 cm to the right of the response disk, 0.2 cm above the bottom of the cage. A photosensor detected entries and withdrawals from the hopper. A baffle covering the top half of the hopper prevented a mouse from fully entering the hopper.

A white 24-volt bulb (GE 1219) mounted above the disk and behind a translucent Plexiglas cover served as a houselight. A Sonalert® audio device, mounted to the right of the houselight and outside the chamber generated a 2900 Hz 70-dB tone whenever the houselight was turned on. A ''Labmaster'' (Scientific Solutions, 938193) card and custom-built interface connected all eight experimental chambers to a 486 DX2 PC computer and controlled the experiment and collected the data (Zarcone & Fowler, 2001).

Response Definitions and Derived Measures

A *threshold disk press* was defined as a peak force on a disk exceeding 2 g with duration greater than 10 ms. The 2-g threshold was chosen so that electrical and vibrational noise would not be registered as responses. Figure 2A shows six disk presses (peak force > 2 g, dotted reference line) followed by a hopper entry. This panel shows the force tracing exceeding 2 g six times before a hopper entry. *Criterion disk presses* were defined as a force on
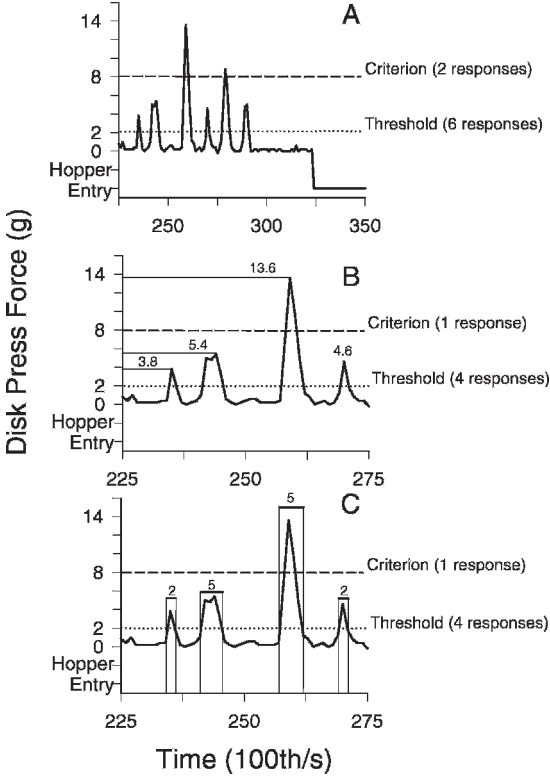

Fig. 2. Diagrams of force tracings for individual disk presses sampled at 100 Hz. Panel A shows six threshold responses followed by the beginning of a hopper entry. The y axis shows disk-press force in g, and the x axis shows time in 100th/s. A Threshold disk press was counted when the tracing exceeded the 2-g requirement marked by the dotted line. A Criterion disk press was counted when the tracing exceeded the 8-g requirement marked by the dashed line. In this sample, six threshold responses are shown, two of which met the force requirement. A solid reference line shows which responses are highlighted to show peak force and response duration in panels B and C. Panel B shows the first four responses from panel A. The number above each peak shows the peak force for that response in g. Reference lines are drawn for the first three responses to the corresponding level on the y axis. In this panel four threshold responses were made and only the third response met the force criterion. Panel C is the same as panel B, but the response duration is given for each response and the reference lines highlight the start and stop times.

a disk exceeding an experimenter-defined force requirement (in this sample the criterion was 8 g) with duration greater than 10 ms. Criterion disk presses are a subclass of threshold disk presses. Figure 2A shows that two of the six responses (third and fifth) exceeded the 8 g force requirement (dashed reference line). Disk-press *peak* force was

defined as the highest force value reached between the start and the end of a threshold disk press. Figure 2B shows the peak of the first four responses from panel A. Disk-press *duration* was measured from the time the force exceeded 2 g and ended when the force was less than 2 g for more than 10 ms. Figure 2C shows the duration of the first four responses from panel A. The *time-integral of force* was the area under the force–time curve and was estimated by the sum of each force sample (100 samples/s) across the duration of a disk press (see Figure 2C) and is indicative of the total amount of energy expenditure for a response (Notterman & Mintz, 1965).

Procedure

Training. Each mouse was first adapted to the chambers for three 30-min sessions, and then trained under an automated disk-baiting procedure for eleven 30-min sessions used to establish disk presses. During the disk-baiting sessions, milk was smeared on the response disk and an FR 1 contingency was in place for responses that exceeded a 2-g force (see Zarcone, Chen, & Fowler, 2004, for details).

Operant sessions. Prior to each session, the houselight and sonalert stimuli were manipulated to examine potential anticipatory behavior. The houselight and sonalert were off during the first 10 min. For the next 10 min, the houselight and the sonalert cycled on 1 s, off 1 s. Then the houselight and the sonalert remained on continuously for another 30 s. No reinforcers were presented during these presession conditions. The mice made disk presses and hopper entries during these presession periods that increased in frequency up to the start of the reinforcement period described below. The data for these presession periods are not reported here in order to focus on the main purpose of describing the relation between force requirements and reinforced operant responding.

The session itself was signaled with the houselight and sonalert turned on continuously while a FR 1 schedule was in effect for 30 min. There was no limit on the number of reinforcers that could be obtained. During the FR 1 schedule, disk presses above the programmed force criterion raised a dipper containing the milk solution into the hopper for 5 s. There were no other stimulus changes signaling that the response criterion had been

Table 1

Number of sessions under each ascending series of criterion-force requirements.

	Number of sessions	
Force Criterion (g)	Exposure 1	Exposure 2
2	18	5
4	5	5
8	5	5
16	10	10
32	5	5

met other than the operation of the dipper, which was accompanied by the sound and vibration of the solenoid operation.

Table 1 summarizes the criterion-force conditions under FR 1. Two replicate ascending series of requirements were studied. In Exposure 1, after 18 sessions with a 2-g criterion-force requirement for disk presses, the force requirement was increased to 4 g for five sessions, 8 g for five sessions, 16 g for 10 sessions, and finally 32 g for five sessions. Exposure 2 repeated the sequence, with the exception that the 2-g criterion was employed for only five sessions.

RESULTS

Disk-press force representative samples. Figure 3 shows event record samples of individual disk presses. These responses were made during the last sessions of the second exposure of the 4, 8, 16, and 32-g requirement conditions by 2 mice. Each panel shows a 2-s record sample from a separate session, one record for each of the different force requirements. Samples from the 2-g requirement are not shown because they did not differ from disk presses made during the 4-g requirement phase. A typical press to a disk resulted in a spike with a steep increasing slope that peaked and rapidly decreased toward zero. For the 4-g requirement (first column), note that the actual force emitted exceeded the requirement and that mice made more than one response even though the reinforcement contingency was FR 1. At the 8-g requirement (second column), mouse CD-1 01 emitted forces twice as high as the programmed force requirement. At the 16- and 32-g requirements (third and fourth columns), CD-1 mice also emitted criterion-level responses. Across the criterion-force conditions, most mice made multiple threshold and/or criterion disk
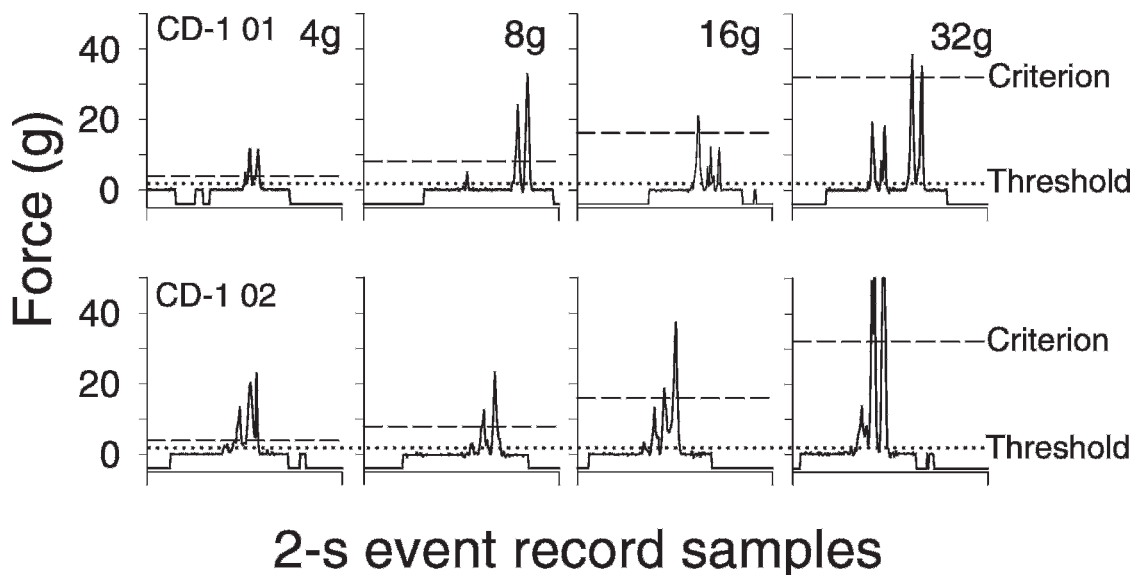
Fig. 3.   Individual response samples for two CD-1 mice during the last session of the 4-, 8-, 16-, and 32-g requirements of the second exposure. Each panel shows a 2-s event record sample from a separate session, one event record for each of the different force requirements. Samples were taken from the first 2 min of each session and are typically the third or fourth reinforced response of a session. The y axis is expressed in gram-equivalent weights, and the length of the x axis is 2 s. All panels have the same x- and y-axis ranges. Dashed horizontal lines designate the force requirement; dotted horizontal lines designate the threshold. A zero reading shows that no force was being applied to the disk. A reading below zero (i.e., −20) designates a hopper entry. A reading above zero indicates an increase in the force applied to a disk.

presses for each reinforced hopper entry. Note that the basic form of a disk press was retained with multiple presses being made for each hopper entry.

Most of the samples show increased peak force with successive disk presses. An additional response characteristic is revealed in the force tracings for mouse CD-1 02. This mouse showed single responses with multiple peaks. For example, the third panel from the right shows three responses, but four peaks. The first two peaks are defined as individual responses because the force exceeds 2 g and then falls below 2 g after each peak. The third and fourth peaks are part of a single response because the force does not fall below 2 g after the third peak and did not meet the criterion for a completed response. It is not until after the fourth peak that the force falls below 2 g and the reinforcement contingencies have been met and the dipper raised. Another important feature is that the forces represented in the panels on the far right (32-g requirement) are above the animal's body weight, which was approximately 30 g under these dietary restrictions.

Threshold and criterion response rates.   Figure 4 shows that rates of threshold responses were relatively stable by the end of the 2-g training phase. Because criterion responses are a subclass of threshold responses, the criterion rate will always be lower than the threshold rate, except when threshold equals criterion. On the first introduction to the 4-g requirement, the CD-1 mice showed lower threshold and criterion response rates compared to the 2-g requirement phase. Inspection of event records showed that some mice were making threshold disk presses that did not meet the force requirement followed by long hopper entries. These events occurred several times before disk-press forces met the new reinforcement criterion. To determine if hopper entries changed during this decrease in response rate, hopper rates and duration were compared to response rates for individual mice. Paired t-tests of each of these variables across days showed statistically significant differences at the $p < 0.05$ level. Hopper rate was lower on the first day, but on the second day hopper rate increased for all mice except 6 and 12. Hopper duration remained constant across
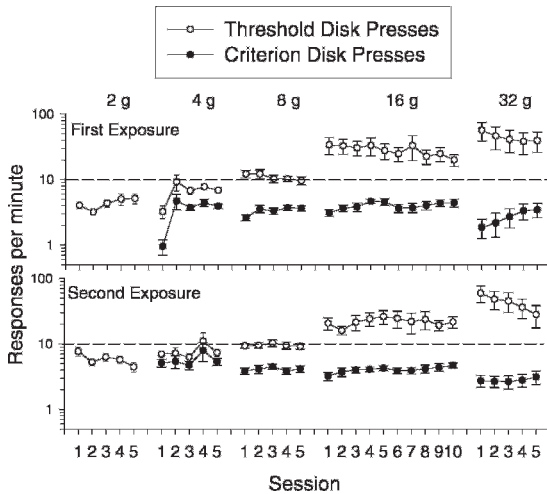
Fig. 4. Response rates for all threshold responses (open circles) and criterion responses (closed circles) as a function of session during the first exposure (top panel) and second exposure (bottom panel) to the different force-requirement phases (2, 4, 8, 16, and 32 g). The y axis is logarithmic, and the error bars indicate the standard error of the mean (SEM). For the 2-g requirement, threshold and criterion responses are the same.
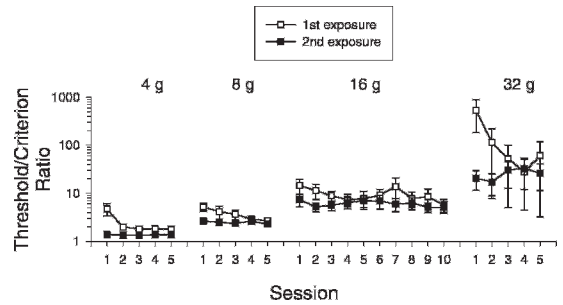

Fig. 5. Ratio of threshold to criterion responses as a function of session. Open squares show data from the first exposure, and filled squares show data from the second exposure for force requirement phases 4, 8, 16, and 32 g. The y axis is logarithmic. For the 2-g requirement, threshold and criterion responses are the same (i.e., the ratio equals 1 by definition).

both days for all mice except 9, 10, and 11. These 3 mice showed average hopper durations around 12 s on the first day that decreased on the second day to the same duration as the other mice. Disk-press rate for these 3 mice were also the lowest on the first day of the 4-g requirement. Mouse 03 also had low disk-press rates on the first day, but did not show long hopper durations. When the data for mice 9, 10, and 11 were removed, none of the paired t-tests were statistically significant at the $p < 0.05$ level.

Changing to the 8-g requirement resulted in an increase in rate of threshold disk pressing and a decrease in rate of criterion disk pressing (Figure 4). Across the 8-g phase, criterion disk presses increased, with a small but detectable decrease in threshold responses. Changing to the 16-g requirement also resulted in increases in threshold disk-press rate and decreases in criterion disk-press rate, followed by a decrease in threshold rate and increases in criterion disk-press rate across the 16-g phase. The 16-g requirement was extended for five additional sessions, but did not show much change in response rates for either criterion or threshold responses. Introduction of the 32-g requirement decreased

criterion disk-press rate and increased threshold disk-press rate. Additional sessions at the 32-g requirement resulted in an increased rate of criterion responses and decreased rate of threshold responses.

During the second exposure under the 2-g requirement (Figure 4, bottom panel), disk-press rate was comparable to that in the first exposure. During the second 4-g requirement the CD-1 mice emitted similar threshold disk-press rates, but had an increased proportion of criterion disk presses. For the remainder of the force requirements (8, 16, and 32 g) the mice emitted similar threshold and criterion rates as those seen in the first exposure.

Figure 5 shows the ratio of criterion responses to threshold responses across sessions for each of the force requirements above 2 g for each exposure. These ratios are the actual variable-ratio schedules experienced by the mice even though the experimenter-defined reinforcement criterion was a fixed ratio 1 for the different force requirements. The higher the value of this measure, the more threshold responses were emitted per criterion response. For the first session of exposure to the 4-g requirement, there were more than four times as many threshold responses as criterion responses (i.e., 4:1). This ratio decreased to ~2:1 for the remainder of this phase. Increasing the force requirement to 8 g increased the ratio to 5:1 during the first session, but produced a gradual decrease of the ratio to ~2:1 with repeated sessions. The ratio increased to ~14:1 during the first session of the 16-g requirement, but gradually decreased
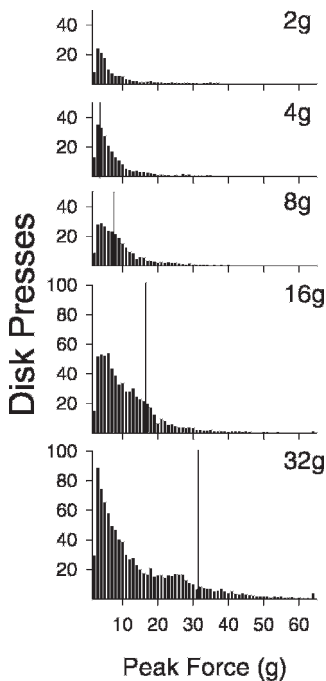
Fig. 6. Group frequency distributions of disk presses for the last session of each force requirement during the second exposure. The vertical lines designate the force requirement; all data to the right of the vertical line represent criterion responses. The y axes for the 2-, 4-, and 8-g panels have been cropped for clarity, but are the same scale as the panels for the 16-g and 32-g phases.

Fig. 7. Frequency distribution samples of disk-press forces for individual CD-1 mice (01–first column and 03–second column) during the last session of each force requirement (2, 4, 8, 16, and 32 g) during the second exposure. The vertical lines designate the force requirement; all data to the right of the line represent criterion responses. The y axes are different for each mouse, but the same across phases.

to ~5:1 by the end of this phase. The initial 32-g force requirement session produced a ratio of ~532:1 with a decrease in the ratio with repeated sessions (~30:1). The second exposure did not show the initial high ratios seen with the initial first session exposures, but the ratio of threshold to criterion responses did increase with the increase in the force requirement.

Peak force distributions. Figure 6 shows peak force distributions during the second ascending force requirement conditions (2, 4, 8, 16, and 32 g) for the last session of each of these phases. The mice emitted peak forces greater than the 2-g requirement with a mode at 3 g. Some mice emitted peak forces up to 40 g. Under the 4-g requirement the mice still showed a mode at 3 g, with 84% of the responses meeting the force requirement. At the 8-g requirement, the mode increased to 4 g, with 55% of the responses meeting the force requirement. At the 16-g requirement the mode increased to 6 g, with 25% of the
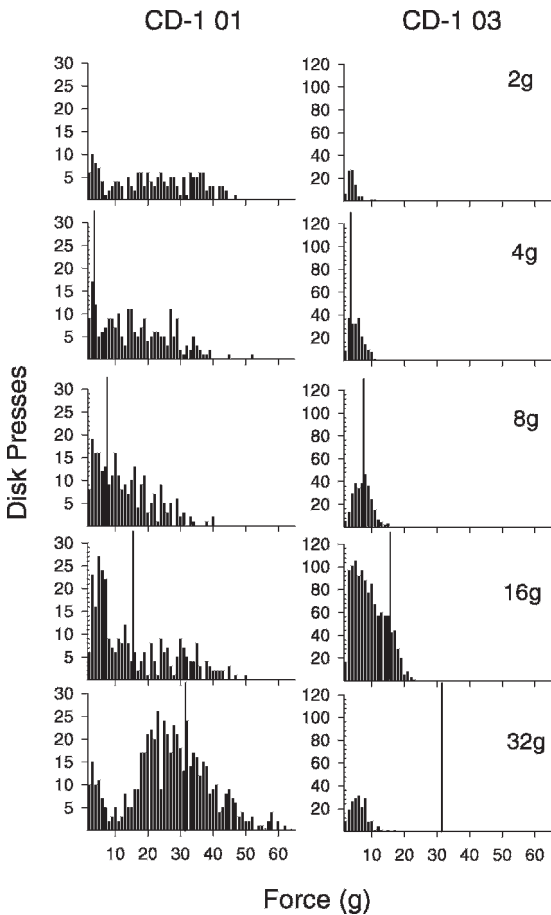
responses meeting the force requirement. For those mice responding at the 32-g requirement, the mode decreased to 3 g, with 12% of the responses meeting the force requirement. Overall, the higher the force requirement, the more responses were emitted, but fewer responses met the force requirement.

Individual differences within group. Figure 7 shows sample frequency distributions for two mice (01 and 03) for the last session of each phase. These mice were chosen to demonstrate the differences in individual response distributions that can be obscured by group averaging. Note that the y-axes of these graphs
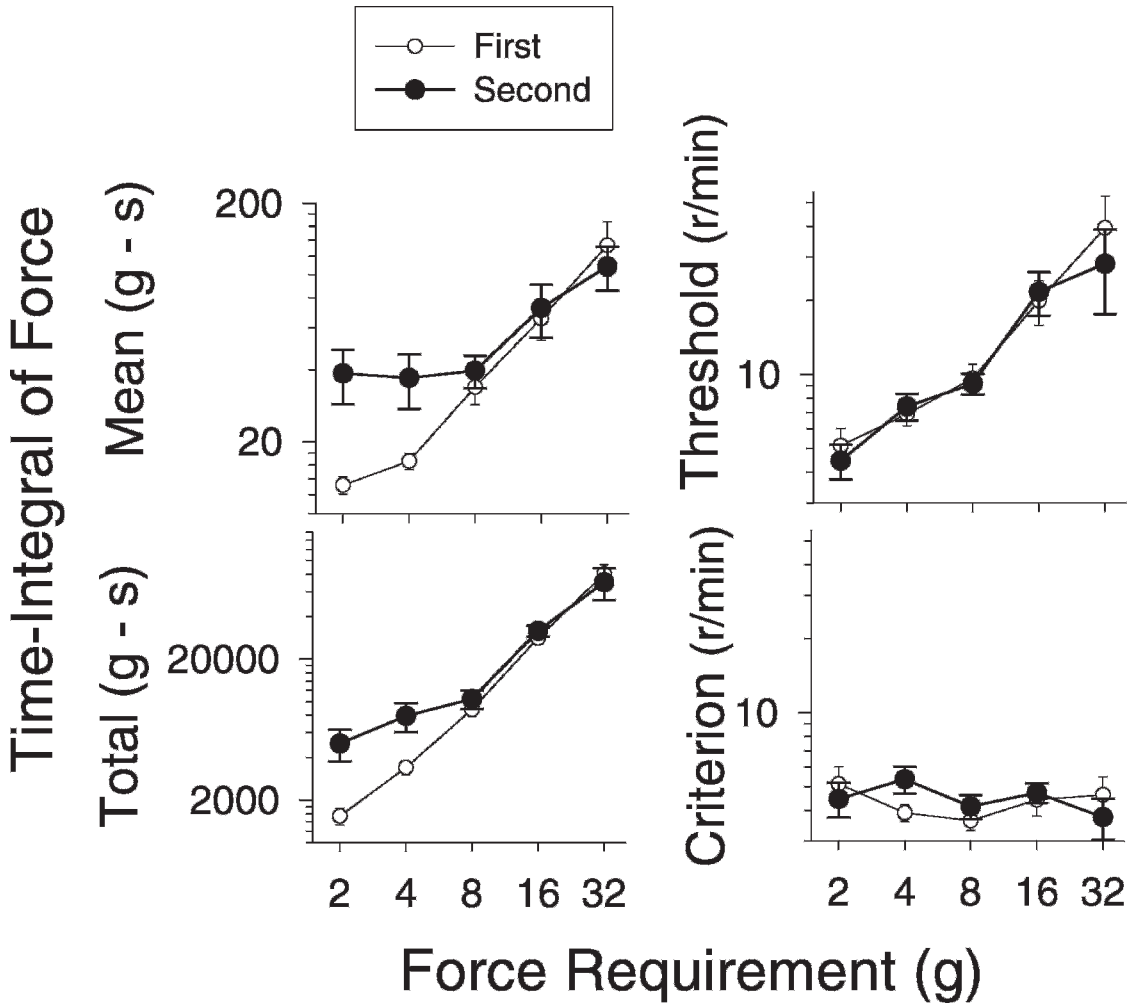
Fig. 8. Average and total time integral of force (left panels) and threshold and criterion response rates (right panels) as a function of the first (open circles) and second (filled circles) exposures to the force requirement (2, 4, 8, 16, and 32 g). Data points were calculated from the last session of each phase.

are different between mice. Compared to mouse 01, mouse 03 had a more constricted distribution that shifted to the right (higher forces) with the increase in the force requirement but did not make criterion disk presses at the 32-g requirement.

Time integral of force (∫F dt). Figure 8 shows the mean and total ∫F dt measures of responding for the last session of each force requirement phase for both the first and second exposures. The mean ∫F dt describes the typical amount of effort per response emitted, whereas the total ∫F dt provides an estimate of the entire amount of effort emitted during a given period. The upper left panel of

Figure 8 shows that the mean ∫F dt increased with increases in the force requirement. These data show that, on average, the ∫F dt increased with increases in the force requirement and remained elevated after exposure to higher force requirements when the force requirement was lowered (see differences between first and second exposure for the 2- and 4-g requirements). The lower left panel of Figure 8 shows that the total energy output for a session also increased as the force requirement increased, and that a history of responding under higher force requirements changes responding at lower response-force requirements. These data show that the mice contin-

ued to expend more effort, both for individual responses (mean $\int F \, dt$) as well as for the entire session (total $\int F \, dt$) at lower force requirements after experiencing higher force requirements.

Analysis of threshold and criterion response rates (Figure 8, right panels) showed that threshold responses increased while criterion response rates remained relatively constant with increased force requirements. The second exposure to the force requirements produced comparable threshold and criterion response rates. The important feature of the panels in Figure 8 is that threshold response rate increased along with mean and total $\int F \, dt$, whereas criterion response rate did not, showing that criterion response rate underestimated response force output. Even threshold response rate underestimated response force output after exposure to the higher force requirements increased the mean $\int F \, dt$.

DISCUSSION

The present analysis of threshold and criterion responses under different force requirements showed that threshold response rates increased with increases in the force requirement. Criterion response rates temporarily decreased with each force requirement increase, but returned to previous levels with successive sessions. The present data replicate previous research by Notterman and Mintz (1965) who measured threshold and criterion responding by rats and showed that changes in the force requirement changed the relative frequency distributions of peak force of responding. They also showed that not all emitted responses (threshold) are reinforced under continuous reinforcement schedules. The present experiment, however, did not replicate previous results showing that criterion responding decreased with increased force requirements (Adair & Wright, 1976; Alling & Poling, 1995; Chung, 1965; Mowrer & Jones, 1943). The additional measurement of threshold responses in the current report shows that threshold responses increased while criterion responses remained relatively constant when the force requirement increased.

One explanation for the lack of observed decreases in criterion response rates may be that the force requirements used in the present experiment were not sufficient to produce aversive consequences capable of suppressing all disk presses. However, comparison of the force requirements relative to body weight shows that the forces used in the present experiment were comparable to those used by Alling and Poling (1995). Adult male Long-Evans rats at 85% of their free-feeding weight weigh approximately 320 g. The force requirements of 25, 50, 100, and 200 g used by Alling and Poling were approximately 7, 15, 31, and 62% of the rats' estimated body weight. Adult CD-1 male mice at 85% of their free-feeding weight weigh approximately 32 g. The force requirement of 2, 4, 8, 16, and 32 g were 6, 12, 25, 50, and 100% of the body weights. Although the comparison of force requirement to body weight does not prove that forces were equivalent between the two studies, this comparison suggests that any aversiveness associated with force increases was not substantially different between rats and mice.

Another possible explanation for the different results may be in the methods used to manipulate force and measure responses. For Alling and Poling (1995) the force requirement was manipulated with an electromagnet and the metal shaft of a response lever. Increasing the current through the electromagnet increased the amount of force needed to separate the metal shaft from the magnet in order to travel 0.2 cm and operate a microswitch. When no current ran through the electromagnet the response requirement was 0.25 N or 25 g. However, when the magnet was turned on and higher forces were required to release the metal shaft from the magnet, the response dynamics changed so that the initial force had to exceed the requirement, but once the connection to the magnet was broken, the force required to travel 0.2 cm returned to 25 g. This action would cause a sudden acceleration in the displacement of the lever followed by the impact of the metal shaft contacting the stop of the microswitch. The aversive qualities attributed to the force requirement may actually be due to the sudden changes in acceleration and not the force requirement.

Similar effects may be occurring with response force manipulations of keypecking by pigeons (Chung, 1965). In this situation the form of the response is more ballistic, and increases in the force requirement would

require more violent head acceleration to move the key the required distance to activate the key. An alternative key-press topography would be to place the beak against the key and lean on the key so that the animal's body weight is used to move the key the required distance. This topography change would also limit response rate, because more time would be involved in using the entire body to complete the response. This rate limitation due to change in response topography also could occur with lever pressing (Adair & Wright, 1976; Alling & Poling, 1995; Mowrer & Jones, 1943).

Under the lowest force requirements, a response lever can be depressed with one forepaw to activate the microswitch. Once the force requirement is changed, the subject is free to change the topography of its response to again activate the microswitch. One strategy for higher force requirements is to use both paws or bite the lever and lean on the lever, using body weight, to help activate the microswitch. Changing the topography of responding also may increase the amount of time needed to complete a response. That is, it takes longer to rear up, place both paws on the lever, and then lean on the lever under the 200-g requirement than it is to reach up with one paw and press the lever using only the shoulder and arm muscles under the 25-g requirement. This type of response topography change in the lever-press arrangement is minimized in the disk-press arrangement due to the limited access to the operandum.

Initial exposure to the 2-g requirement produced group average response rates between three and five presses per min, and changing from the 2- to the 4-g requirement for the first time produced a group decrease in threshold and criterion response rates for the CD-1 mice (Figure 4). These response rate reductions were a result of some mice making threshold responses, which did not raise the dipper, followed by hopper entries with long durations (~12 s). This phenomenon was limited to a small portion of the group (3 of 12), but because the difference in hopper duration was so large for these 3 mice, the effect was statistically significant. Additional changes in the force requirement did not result in decreases in threshold response rates.

Continued exposure to a new force requirement resulted in a lower threshold-to-criterion response ratio. The experimental design, however, did not require that steady-state performance be established prior to changing the force requirement. Whether further decreases in the threshold-to-criterion ratio would have resulted with additional sessions is not known. Changes in the force requirement were evident during each phase with either decreases in threshold response rates or increases in criterion response rates or both.

Threshold responses, while not meeting the conditions for reinforcement or measurement, may still be considered responses that belong to that operant class (Catania, 1998). The measurement of threshold disk presses shows that the mice continued to interact with the operandum even though these responses did not meet the reinforcement criterion. Micro-analysis of the individual responses (Figure 3) showed that many criterion responses were preceded by a series of threshold responses. These data suggest that previous reports of response rate decreases (criterion responses only) and interresponse time increases may be due to increases in subcriterion responses (i.e., above-threshold, but below-criterion, responses).

Subcriterion responses, whether they occur before or after a criterion response, also are reinforced due to the temporal contiguity with the reinforcer, probably in proportion to the temporal distance from the reinforcer (e.g., by a yet-to-be-determined decay function). It would appear that most operant responses recorded by switch activation in laboratory animal operant chambers, as well as most naturally occurring reinforcement situations, are subject to this unintended reinforcement of responses that fall below the force needed to register as a criterion response. There are many dimensions in which behavior may deviate from the target response (e.g., topography, location), and the response-force dimension appears to be a convenient one for measuring some of the characteristics of noncriterion responding that contribute to the rate of the target response. Despite the apparent inefficiency of subcriterion responding, emitting behavior that deviates from the target response may have biologically adaptive properties. In a laboratory setting, during a schedule of positive reinforcement, when an animal makes any subcriterion response, it

may ''discover'' that the environment may have changed to allow less effortful responses. In the natural environment, the variation represented in the force (or other dimension) distribution provides the instances from which new behavior may be selected.

The group peak force distributions from the present experiment show that when the force requirement was low, most threshold responses emitted were reinforced, but as the force requirement increased (8-g requirement and above) the increasingly frequent threshold-only disk presses were not followed by milk presentation. Increasing the force requirement for a single criterion response (FR 1) may be similar to introducing an intermittent schedule of reinforcement. For example, as with variable-interval schedules, in which the time since the last reinforcer presentation is the only constraint on reinforcer presentation, responses that occur during the interval have no experimenter-defined consequences and are free to vary. Increasing the force requirement in a FR 1 schedule also introduces a delay between reinforcer presentations since previously reinforced response-peak forces undergo extinction and eventually lead to a higher peak-force response, which is reinforced. The higher force requirement produces bouts of responding in which the peak force of a response increases with each successive response until the peak-force requirement is met. Notterman and Mintz (1965, pp. 175–182) showed similar response characteristics using fixed- and variable-interval schedules. It is probably the case that FR 1 is only a nominal description of a procedure that might have functional consequences for traditionally unmeasured (and uncounted) members of an operant class that determine the rate of measured (and counted) members of an operant class.

The development of technologies to manipulate genetic material and expression in mice has led to increased interest in the use of behavioral technologies with this species (e.g., Baron & Meltzer, 2001; Wenger, Schmidt, & Davisson, 2004). Many of the studies that look for genetic influences compare groups of genetically defined mice (e.g., wild-type, heterozygous, vs. homozygous). This method of comparison requires the averaging of data between mice types for statistical analysis. A similar approach was taken here, and group averages of response

rates and force distributions were presented. In addition, samples of individual force distributions revealed a considerable amount of within-group variability in the response distribution despite relative homogeneity in the average response rate. These observations suggest that even relatively simple procedures like FR 1 for disk pressing can produce a wide range of response-force distributions.

The use of an isometric disk-press operant with mice is unique. Key presses have been used more often with pigeons (e.g., Ferster & Skinner, 1957). However, the disk press in the present experiment also shares features with the hole-poke response more frequently used with mice (e.g., Wenger et al., 2004). The disk-press apparatus used in the present study is similar to a hole poke in that the force-sensitive disk was recessed behind a hole in the intelligence panel. A disk press differs from a hole poke in that either there is nothing for a mouse to contact on the opposite side of the hole or there are no response-force requirements if there is a contact surface as part of the hole-poke operandum. Despite these differences, results with the disk-press apparatus may have relevance to hole-poke procedures due to the similar topographical features of responding on these two operandi.

The present experiment showed that over the range of increasing force requirements, the peak-force distribution was skewed with the modal peak near the system threshold (2 g), while the rate of disk pressing increased. These results suggest that disk-pressing—and possibly hole-poking—topographies may not be completely free from other controlling variables. For example, mice typically investigate their surroundings via the sensory organs located on the snout (olfactory nerves and vibrissae) and position these sensory organs so as to contact an object to maximize odor stimulation and physically move the vibrissae. The topographies involved in these sensory functions are similar to the definition of a disk press or hole poke and may be responsible for the high rate of low force disk presses observed in the present experiment.

Using the concept of least effort as an explanation for changes in response rate appears to also require independent measurement of energy expenditure. Data from the present experiment show that even though

criterion response rates eventually were maintained across force requirements ranging from 2 to 32 g, energy expenditure estimated by the integral of force measure increased with the response-force requirement. Responding during the second exposure to the 2- and 4-g requirements showed that mice made more effortful responses despite the lower force requirement, even though threshold and criterion responses rates were similar to the first exposure. These data suggest that at low force requirements, response force may not be subject to the constraints suggested by the concept of least effort. As for high force requirements, changes in response rate may be due to increased time to complete new response topographies or the production of aversive consequences with response topographies involving sudden changes in acceleration and deceleration.

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